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BIOLOGICAL BULLETIN.

ABNORMALITIES IN THE CESTODE MONIEZIA EXPANSA. III.

(*Continued.*)

3. ORIGIN OF THE ABNORMALITIES.

The preceding description has rendered it evident that the process of proglottid-formation begins deep within the body and only gradually becomes visible on the surface. The external features of the proglottids, their contours and the furrows which appear between them are only indications of the localized growth that has taken place within the body. Since the primary region of proglottid-formation is the central parenchyma, and the process extends only secondarily to the peripheral parenchyma, it is theoretically possible that a proglottid might be formed in the central parenchyma without becoming visible on the surface as an area of localized growth bounded by furrows. There is some evidence that such a condition occasionally exists. Its discussion is postponed to a later section of this paper. In general, however, the furrows and their external features are simply the visible signs of internal processes of certain kinds and intensities. This being the case, variations in form and structure of the proglottid are the consequence of variation in the formative processes.

(a) *Variation in Form of Proglottids.*

The division of the variations into two groups, non-spiral and spiral variations, which was adopted in Parts I. and II., is retained here for convenience. The imperfect or partial proglottids are considered first as showing the simpler forms of variation. A study of the abnormalities of this group shows very clearly that all are simply incompletely developed proglottids, either fused with others or separated from them by furrows.

Part I. (Child, 'oo) was devoted to the description of cases of this kind and the Figs. 2-23 show a large variety. Bearing in mind the method of formation of each proglottid from the two distinct lateral groups of nuclei in the central parenchyma, *i. e.*, from two separate right and left halves which later become united, it is not difficult to understand how the conditions represented in Figs. 2-23 have arisen.

The cases which differ least from the normal form are those in which the furrows between two proglottids are interrupted at some point or points (*e. g.*, Figs. 11, 12, 13, 15, 16, etc., Part I.). In these cases the proglottids arose in nearly the normal manner. The growth of the two, however, has not been sufficiently distinctly localized to cause the appearance of complete furrows. The various degrees of fusion are indicated in each case by the extent and distinctness of the furrows and the condition of the genital organs. The furrows on the two surfaces of the body may or may not correspond in cases of this kind, *i. e.*, the growth may be more distinctly localized on one surface than on the other or may be alike on both.

In all of the cases just noted, right and left halves of each proglottid are present, and each must have been represented originally by a more or less distinct group of nuclei. In other cases only the right or left half or smaller fractional portion of the proglottid appears, the remainder not being represented. Such variations are clearly the consequence of the formation and growth of a proglottidal anlage on one side of the neck-region only, no corresponding group appearing on the opposite side (Fig. 18, Pt. I.), or else there are two small groups on one side corresponding to one larger group on the other (Fig. 9, Pt. I.). Whether the partial proglottid is entirely distinct (Fig. 18, Pt. I.) or united with a whole proglottid (Fig. 9, Pt. I.), depends probably upon the time of its formation. If two anlagen are found on one side of the body at the same time that one appears on the opposite side, the two of the one side are likely to become connected with the one of the other, thus producing what appears to be a partial division of the proglottid in the transverse plane (*e. g.*, Figs. 9, 10, etc., Pt. I.). If, however, an anlage appears on one side without any corresponding to it on the opposite side, a partial pro-

glottid wholly separated from all others by furrows will probably be formed (*e. g.*, Fig. 18, Pt. I.). These variations consisting of half-proglottids or smaller fractional portions cannot be sharply separated from the preceding group in which both halves are present, but imperfectly defined. As is evident from the figures, all gradations occur. The one extreme approaching the normal condition consists of two or more well-defined proglottids with scarcely interrupted furrows (*e. g.*, Fig. 12, Pt. I.). In many other cases both halves of each proglottid are present, as indicated by the genital organs, but those of one side, right or left, are not sufficiently distinct to cause the appearance of normal furrows (*e. g.*, Figs. 11 and 16, Pt. I.). In most of these cases one of the imperfectly separated halves is reduced, the reduced portion being always the anterior, *i. e.*, the later in time of formation (Figs. 10 *b*, 16, 17, 19, 21, 22 *c* and *d*, Pt. I.). The opposite extreme is reached in those cases where the proglottid appears only on one side of the body, not being represented in any way on the opposite side (Figs. 9 and 18, etc., Pt. I.).

It should be noted that all imperfect or partial proglottids occur either in the right or left half of the body or in both, never in the middle region only. This fact must be interpreted as indicating that they are the result of imperfect development either of the right or left proglottidal anlage or of both. If the normal proglottid were formed by simultaneous differentiation and growth all the way across the body, there seems to be no good reason why abnormalities should not appear near the median line without reaching the lateral margins as often as they occur in the right or left side. Each proglottid arises, however, from two distinct anlagen placed laterally in the central parenchyma and these unite secondarily at the median plane. Therefore the conditions near the median plane must depend upon the development and growth in lateral regions. On the other hand it will be observed that none of the variations are confined to the extreme margin of the body. All include the region which was occupied by the group of nuclei at the time of proglottid-formation. In the figures this region lies slightly lateral to the ovaries.

It is evident that all the facts concerning position, form, extent, and distinctness of the imperfect and partial proglottids harmonize

with and confirm the observations discussed above, on the development of the normal proglottid.

The examination of imperfect or partial proglottids in the light of the facts gained from the study of normal proglottid-development leads to the following conclusions ; the right and left halves of the proglottid pass through at least the early stages of their development independently ; either or both may remain incompletely developed, as regards size, form, or distinctness, or only certain parts of one or both may develop, or finally one may be wholly absent. All imperfect and impartial proglottids are the result of such incomplete development, and in their manifold forms illustrate a great number of different combinations of the various factors concerned.

A very early stage of abnormal proglottid-formation is illustrated in Fig. 57. The dotted lines drawn through the figure indicate approximately the boundaries of an abnormal region. On the left side two half-proglottids are forming, and corresponding to these on the right is only one. In this case the growth is almost wholly confined to the central parenchyma, so that furrows on the surface are not yet present. Yet I think that there can be no doubt that this region represents an early stage of a condition similar to that shown in Fig. 9, for example. On the other hand, the account of proglottid development has rendered it evident that the zones of nuclei represented in Fig. 57 develop from the lateral groups of early stages. This case forms in some respects a connecting link between the observations upon normal proglottid-development and the facts gained from the study of older, well-developed abnormalities. It is the only case of abnormal form observed at so early a stage.

The spiral modifications of form were described in Part II. (Child, '00) and include Figs. 24-37. The simplest form of spiral is such as appears in Figs. 24, 25 *b* and 26 (Fig. 26 is reproduced as Fig. 72), viz., a single half or fractional proglottid united on one surface with the proglottid posterior to it, or separated by a furrow as in Fig. 24, and on the other surface with the proglottid anterior to it.

It is of course evident that such a short spiral differs only slightly from a fractional proglottid of the sort which is shown in

Fig. 9 (Pt. I.) for instance, the only difference being that in case of a spiral the fractional proglottid unites with different proglottids on the two sides of the body. It appears probable that in such cases a slight difference in time of formation of the dorsal and ventral portions of the proglottid is the cause of the spiral condition. As was pointed out above, the relation of partial

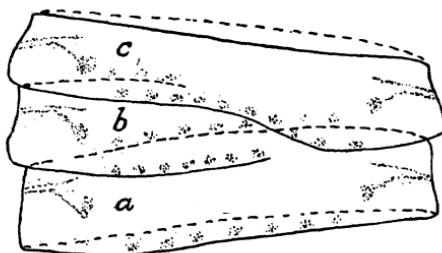


FIG. 72.

proglottids to the proglottids posterior or anterior to them probably depends largely, if not wholly on the time of their formation. If a partial proglottid is formed at the same time as the next posterior proglottid, *i. e.*, a little before normal time, the two will probably be incompletely separated. If the formation of the partial proglottid is retarded slightly it will probably become united with the proglottid anterior to it. And lastly, if the time of formation of the partial proglottid does not correspond to that of any other it will probably be distinct from all others. Applying the same conclusions to the spiral partial proglottids (*e. g.*, Fig. 72) it appears probable that one side of the partial proglottid the dorsal (upper) side of *b* in the figure is formed at about the same time as the proglottid posterior to it, whereas the ventral (lower) side corresponds in time of formation with *c* and so becomes united with it. Recalling the method of formation of the proglottid, it is easy to see that such differences in time of development of different parts are at least theoretically possible. The localization of growth, which is the essential feature of proglottid-formation, may for some unknown reason appear somewhat earlier on one side than on the other, just as it appears earlier in the lateral than in the median regions of the central parenchyma.

If now the dorsal and ventral sides of a series of anlagen on either the right or left side of the body show similar differences

in time of development, a series of spirals may be formed such as appears in Fig. 35 (Pt. II.). If the development of the dorsal and ventral portions of both right and left anlagen is accelerated or retarded the parts show normal relations to adjacent proglottids.

In some cases a form of spiral somewhat different from that just described is produced; in this the furrows on one surface of the body bend either anteriorly or posteriorly near the right or left margin and so unite with other than the furrows corresponding in position on the opposite surface.

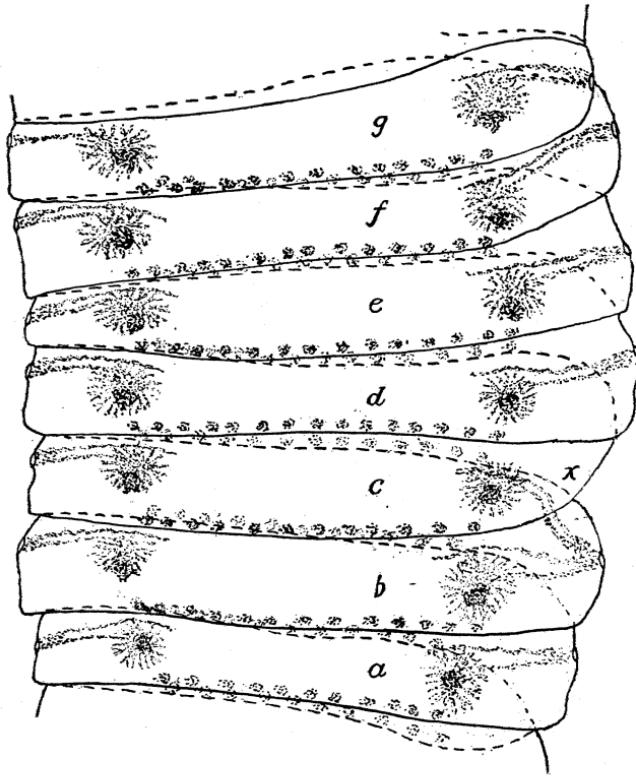


FIG. 73.

The only well-developed case of this kind was shown in Fig. 36 (Part II.). Another case approaching this condition was shown in Fig. 37. These two figures are reproduced here as Figs. 73 and 74. Both are viewed from the dorsal surface. It is evident from the figures that the growth is incomplete in the region

where the furrows bend. In Fig. 73 the curved portions of the furrows near the right margin of the ventral surface are less distinct than the other portions, *i. e.*, growth has been less all along this region of the body. The appearance of the spiral arrangement is connected with the condition of imperfect development. The proglottid *a*, Fig. 73, being the most posterior of the series, *i. e.*, the first formed, is the starting point of the abnormal arrangement. In this proglottid the anterior part of the right ventral region shows a progressive reduction in size with approach to the margin. Now if the same region in each of the following proglottids shows the same imperfect form the anterior boundary

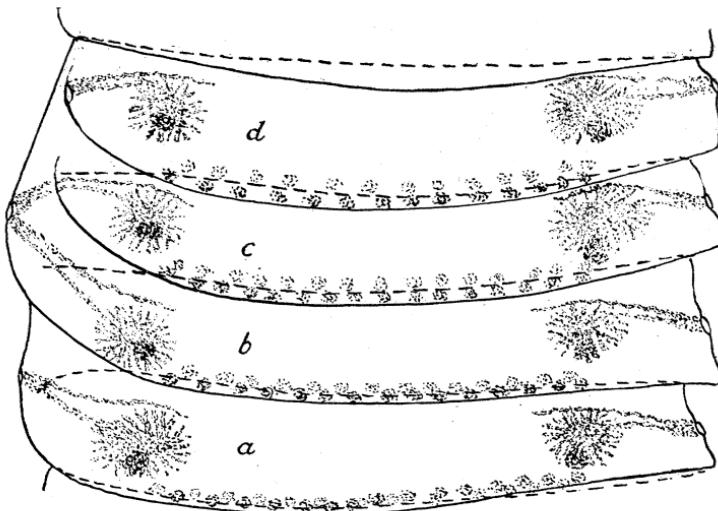


FIG. 74.

will in each case form a curve instead of extending straight to the margin. But the anterior boundary of one proglottid is the posterior boundary of the next anterior; thus the area which would normally be included in *a* becomes the part of *b*, etc. The indistinctness of the curved portion of the furrow is due to the absence of the fold which normally arises at the posterior border of each proglottid. In the regions where the boundary between the proglottids is transverse the fold and inter-proglottidal glands are developed as usual.

In Fig. 74 there is a close approximation to a spiral as the result of incomplete formation of the proglottids. The curve at

the left end of each of the dorsal furrows is clearly due to a progressive reduction and final cessation of proglottidal growth in the region under consideration.

It is the left posterior dorsal portion of each proglottid which has failed to develop fully in this case, while in Fig. 73 it was the right anterior ventral portion. If development in Fig. 74 were complete enough to cause the formation of furrows all the way to the margin a spiral would be formed opposite in direction to that in Fig. 73, simply because of the difference in position and relations of the imperfectly developed regions. But the furrows on the dorsal surface curve to such an extent that they do not reach the margin at all. On the ventral surface there is no reduction of the proglottids, but they are not differentiated at the extreme margin. Consequently the left margin of the region *b-c-d* is not divided into proglottidal regions.

A knowledge of the arrangement of the transverse nerve-commissores in regions of spiral variations of this kind would be most interesting and valuable.

The spiral variations afford further illustrations of the independence of the right and left proglottidal anlagen. In general, the spirals are due to some irregularity in time of growth and differentiation of parts, or to incomplete growth in either the right or left half of the body. A variation of this kind having appeared in a single proglottid shows a certain tendency to reappear on the same side in a number of proglottids (*e. g.*, Figs. 73 and 74).

The condition and development of the furrows cannot be regarded as an exact indication of the conditions in the proglottids which they bound, though a study of the arrangement of the reproductive organs in the abnormal proglottids shows that the furrows do indicate very closely the degree of development or distinctness attained.

But since the earliest stages in proglottid-formation occur only in the central parenchyma, the formation of inter-proglottidal furrows on the surface of the body being a later process, it is evident that a proglottid may attain a certain degree of development without being represented by furrows on the surface. That such cases do actually occur was pointed out in Part I. (*e. g.*, Fig. 10, *b*, p. 226; Fig. 20, *f, g*, pp. 240-241). In Figs. 10, *b*, and 20,

f, g, there is a partial duplication of the reproductive organs, but no furrow between the two sets. Here the causes leading to localization of growth have not affected the outer parts of the body. The genital organs are always reduced in cases of this kind.

Furthermore, it is possible that the furrow may not coincide perfectly with the boundaries of the proglottid in the central parenchyma. The growth in the peripheral parenchyma may be reduced or modified in such a manner as to change the direction of the furrow so that it no longer indicates the exact boundary. A very distinct case of this kind was shown in Fig. 38, Part II., at *m*, and discussed on page 280, and it is possible that the oblique furrow between *c* and *d* in Fig. 38 is another case (p. 283, Part II.).

It is probable that in many cases furrows which curve anteriorly or posteriorly do not correspond to the exact boundaries of the proglottids. Curved furrows of this kind always indicate incomplete development in the peripheral parenchyma, but the central regions may often be more perfectly developed than the furrows indicate.

The preceding discussion of a few typical cases of form-variation in the proglottids renders it sufficiently evident that all of these variations are due to incomplete development of some part or parts, or of the whole proglottid. One of the two anlagen may be absent or may become united with the next anterior or posterior to it. Either or both may fail to attain full size or normal form.

The inter-proglottidal furrows are the chief external indications of internal conditions of growth and development. But the structure of the genital organs in some of the imperfect proglottids indicates a somewhat more nearly perfect condition than that represented by the furrows.

Throughout the whole series of form-variations no new methods of growth or proglottid-formation are indicated. All variations absorbed are simply failures to attain full development. They illustrate very clearly the independent development of each of the two anlagen.

Variations in the form of the proglottids—abnormalities—are extremely common in *Moniezia*, much more so than in most

Cestodes. This condition is perhaps connected in some manner with the fundamental structural or physiological characteristics of the form.

An inquiry as to the causes of the frequency of form-variations in *Moniezia* may therefore concern itself first with the normal anatomy and physiology. A few suggestions as to some of the possible factors concerned are made here in the hope of throwing some light upon this problem. First, the method of formation of the proglottid, its appearance in two separate parts which later unite, must favor to some extent the development of abnormalities, for a slight variation in position or time of appearance of the anlagen may apparently effect the extension and union of the anlagen of the two sides. It is not known at present whether the proglottids of all other Cestodes arise in the same manner. If in some the proglottids originate in a single group of cells the chances for abnormal development would apparently be fewer. Second, the form of the proglottids, the great width in proportion to the length favors the appearance of abnormalities. In the early stages the proglottids are extremely short and it is evident that abnormal union of right and left anlagen must occur more frequently than in forms with longer proglottids. Third, it is possible that the proglottids of *Moniezia* possess a lower degree of individuality than those of some other Cestodes, *i. e.*, that they are less distinct structurally and physiologically. If this is the case then incomplete separation may be expected to occur more commonly than in forms with more highly individualized proglottids.

The frequency of form-variations differs greatly in different specimens. More than half of the cases shown in Parts I. and II. were taken from a single chain and represent only a part of the abnormalities present. Other specimens possess in most cases only a few abnormal proglottids, but nearly every specimen exhibits one or two. We have at present no clue to the cause of this difference. It is possible that age may have some influence, the older specimens showing a tendency to incomplete development. Injuries to the neck-region, or the repeated tearing away of the whole body, or perhaps malnutrition, may also favor the appearance of abnormalities, and finally these differences

may be due not to age or external conditions but to an individual peculiarity. Some may feel inclined to regard this as a reversion to an ancestral condition in which the division of the body into regions of localized growth was less distinct and regular.

(b) *Abnormalities in the Structure of Proglottids.*

Very closely correlated with the variations in form of the proglottids are variations in the structure and arrangement of the reproductive organs. This close correlation was pointed out in detail in all those cases cited in Parts I. and II., in which the reproductive organs were developed. Some points of interest remain to be considered.

The relative position in the proglottid of the various parts of the reproductive organs was noted in Part I. Each portion has a more or less definite relation to the others and to the proglottid as a whole. We might expect that a change in the form of the proglottid would be accompanied either by a modification in the form or arrangement of some part or parts of the reproductive organs, or else, in cases of more extreme variation, that some portions or all of the reproductive organs would be absent. As a matter of fact both of these possibilities are represented.

Considering first the modifications in form and arrangement of the organs without loss of essential parts, we find that considerable departures from the form may occur without apparently interfering with the function of the organs. Two sets of organs may open through a single pore (Figs. 11, 22, *a*, *b*, Pt. I.; Figs. 36, *b*, *c*, 37, *b*, *c*, Pt. II.). In such cases the direction of the ducts in at least one of the sets of organs is distinctly different from the normal direction, being more oblique. In other cases the ducts may run very obliquely toward the margin but without uniting with others (Fig. 33, *c'*, *d'*; Fig. 39, *a'*, Pt. II.). In cases of this kind the ducts may be and usually are much longer than the normal ducts. In other cases the organs may be nearer the margin than normally and the ducts are then shorter than normal. The vas deferens may open directly into the seminal receptacle as in Fig. 21, *c'* (Pt. I.), or two vasa deferentia or two oviducts may unite (Figs. 21, *a'*, 40, 41).

Reduction in size of the female organs and reduction in the

number of the testes frequently occurs in proglottids of less than normal size.

This brief review of these cases only serves to call attention once more to the fact that was repeatedly pointed out in Parts I., and II., viz., that the form and arrangement of the reproductive organs may vary widely in correlation with variations in form of proglottid.

In case the form-variation is extreme, however, parts of the reproductive organs may remain undeveloped and these parts may be those which are essential for the normal functioning of the system. The consideration of these cases leads to the very important conclusion that the development of each part of the reproductive organs shows a very close correlation with the development of the particular region of the proglottid in which it lies. This was pointed out repeatedly in Parts I. and II., and it is not necessary to go over all the particular cases again.

The different conditions represented are manifold. Apparently any portion of the organs may fail to appear as this or that portion of the proglottid fails to develop fully. In case the dorsal side of the proglottid is distinct and the ventral is not, only the vas deferens and testes appear, these lying in the dorsal region of the proglottid (Figs. 16, *b'*; 17, *b'*, etc., Pt. I.). If the ventral side only is distinct from the adjacent proglottids only the female organs or parts of them appear (*e. g.*, Fig. 22, *d*, Pt. I.). Ovary, testes, and, in some cases, the inner portions of the vas deferens and vagina¹ may be present, but if the marginal region is dwarfed the middle, or terminal portions, or both, of the ducts may be entirely absent, or present only in part (*e. g.*, Fig. 39, *b*, Pt. II.). And finally, in extreme cases the reproductive organs may be represented only by one or two small groups of cells in the region where the ovary or vitellarium would appear if present (Fig. 18, Pt. I.).

It is rather common in cases of this kind to find a marginal pore and perhaps the cirrus present but entirely unconnected with the inner portions of the reproductive organs. Either the ducts

¹In Parts I. and II. the designation "oviduct" was incorrectly applied to the whole female duct, including the vagina. Of course the oviduct proper is only a small portion of this. I do not think that my use of the word was such as to cause confusion in this particular case, but I desire to call attention to the error.

leading to the pore are undeveloped (Figs. 22, *d*, Pt. I.; 39, *b*, Pt. II., etc.), or else they open through another pore (Fig. 21, *a'*, Pt. I.; Fig. 40, *b*, Pt. II., etc.). There is in these cases no indication of any morphological connection between the pore and any other parts that may be present, but it may be that the presence of the internal reproductive organs favors in some manner the formation of a pore (though not essential). While this condition occurs so commonly, its complement, development of the middle portions of the ducts without a pore at their outer end or the internal organs at their inner end, has never been observed by me. Thus there is apparently a certain tendency for the organs in the central parenchyma and the marginal pore to appear, even without connection, while the middle portions of the ducts never develop alone. In other words the central parenchyma and the margin are regions of "least resistance." I think the absence of the middle portions of the ducts in so many cases may be due in part to the fact that these portions traverse the thick muscle layers which lie between the central and peripheral parenchyma. The ducts, like the other portions of the organs, appear first as aggregations of parenchyma-nuclei in a mass of undifferentiated cytoplasm. Very few or none of these nuclei exist in the muscle layers. Those portions of the ducts which penetrate the muscles appear normally somewhat later than the outer and inner parts, apparently because the material is less abundant here and probably also because the muscle-layers offer a certain degree of resistance to the penetration of the ducts. Apparently either the outer or inner portions or both grow into the muscle-layer and so become continuous. Now it is extremely probable that if any tendency to incomplete development of the reproductive organs exists in the lateral regions it will show itself first in the region where material is least abundant and growth apparently most difficult, *i. e.*, in that portion of the ducts which lies in the muscle-layers. This portion might, therefore, fail to appear, whereas the outer and inner parts, lying in regions where material is more abundant and where no special resistance to growth exists, probably do not require so strong a stimulus for their development.

The various abnormalities in the reproductive organs afford

very strong evidence in favor of the view that the principal parts of the system develop independently. A glance over the figures will show that almost any portion of the organs may be present alone. As noted above, the middle portions of the ducts never appear alone and it may be that the ovary and vitellarium always appear together. The dependence of the middle regions of the ducts on other portions has been discussed. The relation of ovary and vitellarium is perhaps explicable on the view commonly held that the vitellarium represents a modified portion of the ovary. The earliest stage of the reproductive organs is a mass of nuclei in the region where the ovary and vas deferens appear later. This increases in size and gradually differentiates, but the study of the abnormalities renders it very evident that the development of the portion which forms the vas deferens does not depend upon the development of the ovarian portion and *vice versa*, for the one portion may appear without the other, although both appear to differentiate from a common mass. Testes and vas deferens develop independently of each other, for testes appear in proglottids where there are no vasa deferentia (Fig. 39, *b*; Pt. II.) and *vice versa*. And finally, the pore and terminal portions of the ducts develop independently of the other organs. In the normal proglottids the group of nuclei representing the pore, cirrus, etc., is entirely unconnected in early stages with the group representing the inner organs and may appear alone (Fig. 19, *b*; Pt. I.). The connecting portions of the ducts appear later, as was mentioned above.

We must conclude, therefore, that the lateral reproductive organs are formed from at least three distinct "centers" or regions of independent growth. These may be called the vas deferens region, the ovarian region, and the terminal region. There may be others besides these. In addition, the testes develop in the central parenchyma independently of each other and of the lateral organs. All cases of the incomplete development of the reproductive organs are to be regarded as due to the incomplete development or total obliteration of one or more of these regions.

It is important to note that in all cases of partial development the portions of the reproductive system present show approximately the same degree of differentiation as the corresponding

parts in adjacent normal proglottids, so that it is possible to determine in the older proglottids just what parts are represented in each case. Evidently then there is no great amount of retardation in development in the partial or otherwise abnormal proglottid. Organs once formed develop with the same rapidity as those under normal conditions. What is lacking in these abnormal proglottids is the initial stimulus or the proper condition for the *formation* of this or that portion. The structure of each abnormal proglottid is as complete as possible for that particular form of proglottid. Organs are formed at the same time as in other proglottids and those organs which do not appear at the normal time are not formed later. There is no decrease in the rapidity of development, there is simply the presence or absence of a certain form and correspondingly the presence or absence of a certain structure.

In Figs. 37-41 (Pt. II.) variations of another sort in the reproductive organs are shown. Figs. 37 and 38 both show cases of transverse duplication of portions of the reproductive organs on one side of the body. This abnormal condition does not find a satisfactory explanation in the form of the proglottid. All that can be said at present concerning it is that for some reason an extra growth-center, or perhaps more than one, is formed. In the two cases cited this gives rise only to female organs, in one case (Fig. 38, *b*) to a small imperfect ovary and a few groups of cells representing the vitellarium, in the other (Fig. 39, *c*) to these organs, and, in addition, a small blind seminal receptacle. I have been unable to discover any clue to the causes concerned in the formation of these supernumerary organs.

In Figs. 40 and 41 (Pt. II.) three cases of reversal in position of the lateral organs appear. In Fig. 40 the organs of the right side are reversed in proglottid *b*, and in *d* those of the left side. In Fig. 41 another case of the same kind occurs. This peculiar variation is evidently correlated with the abnormal form of the proglottids. It is, however, difficult to understand why a reversal should occur in these cases, and not in others where conditions are closely similar. It does not seem probable that these variations indicate a "reversal of polarity" in those parts of the proglottids containing them. Considerable variation in the posi-

tion of the organs occurs in normal proglottids. These appear to be extreme cases of adaptation in growth to abnormal conditions.

The inter-proglottidal glands show numerous departures from the typical arrangement and these variations are very closely correlated with the form-variation of the proglottids. The inter-proglottidal glands lie along the posterior border of each proglottid just anterior to the furrow and open into the deepest part of the latter. They are absent near the margins of the body. In general the glands appear wherever even a small portion of a furrow extends beyond the marginal region in which they are never found. The glands never appear except in connection with a furrow, and they appear only along furrows which are transverse or nearly so. In one case shown in Fig. 38 (Pt. II.) the furrow becomes oblique, but the glands tend to continue in a transverse row, and at the anterior end of the oblique portion lie at some distance from the furrow and are connected with it by long ducts, while at the posterior end one gland lies posterior to the furrow instead of in its normal position anterior to it. With respect to this case the suggestion was made on page 283, Part II., that the rows of glands may coincide with the proglottidal boundaries while the oblique portion of the furrow does not. The glands tend to form along the boundaries but apparently do not form at all unless a furrow is present.

The numerous variations which have formed the subject of this paper have demonstrated very clearly the close relation between form and structure. It remains for us to consider whether the variations in structure are the result of the form-variations or whether some common cause underlies both.

The organs of the proglottid appear considerably later than the proglottid itself. If variations in their form and arrangement are due to the same causes as the variations in form of the proglottid, these causes must be active after the formation of the proglottid and must affect the development of the organ in such a way as to cause an apparent adaptation to the form of proglottid.

The natural and obvious conclusion is, I think, that the development of the proglottidal organs must depend upon the devel-

opment of those regions of the proglottid in which they lie. Reduction of any given region means reduction in amount of material and in space, and the organs which develop in this region must be affected. The organs of the normal proglottid are the only organs possible under the given conditions of form, size, etc. Change in the conditions must produce alterations in the organs. The correlation between form and structure as shown in the variations is so close that, given a proglottid of a certain form, it would be possible to predict with a considerable degree of accuracy in most cases what the condition and general arrangement of the organs would be. It is scarcely necessary to seek for a common cause for this correlation of form and structure. I think it is sufficiently clear that the variations in form of the proglottids are the cause of the variations in structure and arrangement of the proglottidal organs.

HULL. ZOOLOGICAL LABORATORY,
UNIVERSITY OF CHICAGO, March, 1901.

LITERATURE.

In the references to literature I have followed the plan proposed recently by Bather ('01), viz., the use of the last two numerals denoting the year for all papers which have appeared within the hundred years preceding the paper.

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DESCRIPTIONS OF FIGURES.

FIG. 42. Transverse section through the neck near scolex.

FIG. 43. Transverse section from middle of neck region.

FIG. 44. Frontal section through anterior part of neck.

FIG. 45. Sagittal section near median line from near middle of neck region.

FIG. 46. Diagram indicating the levels from which various figures were taken.

The numbers correspond with the numbers of the figures.

FIG. 47. Neck, in toto, near scolex.

FIG. 48. Neck, in toto, near middle.

FIG. 49. Neck, in toto; formation of proglottids beginning.

FIG. 50. Neck, in toto; proglottids distinct in central parenchyma.

FIG. 51. Neck, in toto; proglottid-formation extending to peripheral parenchyma.

FIG. 52. Neck, in toto; inter-proglottidal furrows distinct.

FIG. 53. Diagrammatic transverse section through neck, indicating the planes of the sections shown in various figures. The numbers correspond with the numbers of the figures.

FIG. 54. Diagram of a portion of the neck-region, indicating the planes of certain sections.

FIG. 55. Section (nearly sagittal) through one side of posterior part of neck.

FIG. 56. Section (nearly sagittal) through one side of posterior part of neck.

FIG. 57. Frontal section, showing early stages in proglottid-formation. The dotted lines enclose an abnormality.

FIG. 58. Sagittal section of a stage in which the inter-proglottidal furrows first become visible.

FIG. 59. Frontal section, showing one side of young proglottids.

FIGS. 60-70. Surface-views and sagittal sections of proglottids of various ages, showing the relative increase in size of different regions.

FIG. 71. Sagittal section, showing an early stage in the formation of the posterior proglottidal folds.

FIG. 72. Reproduction of Fig. 26; a simple form of spiral abnormality.

FIG. 73. Reproduction of Fig. 36; a spiral series.

FIG. 74. Reproduction of Fig. 37. Incomplete development approaching spiral form.